Dynamics of Pink Shrimp (*Farfantepenaeus duorarum*) Recruitment Potential in Relation to Salinity and Temperature in Florida Bay

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ABSTRACT: Progress is reported in relating upstream water management and freshwater flow to Florida Bay to a valuable commercial fishery for pink shrimp (*Farfantepenaeus duorarum*), which has major nursery grounds in Florida Bay. Changes in freshwater inflow are expected to affect salinity patterns in the bay, so the effect of salinity and temperature on the growth, survival, and subsequent recruitment and harvest of this ecologically and economically important species was examined with laboratory experiments and a simulation model. Experiments were conducted to determine the response of juvenile growth and survival to temperature (15°C to 33°C) and salinity (2‰ to 55‰), and results were used to refine an existing model. Results of these experiments indicated that juvenile pink shrimp have a broad salinity tolerance range at their optimal temperature, but the salinity tolerance range narrows with distance from the optimal temperature range, 20–30°C. Acclimation improved survival at extreme high salinity (55‰), but not at extremely low salinity (i.e., 5‰, 10‰). Growth rate increases with temperature until tolerance is exceeded beyond about 35°C. Growth is optimal in the mid-range of salinity (30‰) and decreases as salinity increases or decreases. Potential recruitment and harvests from regions of Florida Bay were simulated based on local observed daily temperature and salinity. The simulations predict that potential harvests might differ among years, seasons, and regions of the bay solely on the basis of observed temperature and salinity. Regional differences in other characteristics, such as seagrass cover and tidal transport, may magnify regional differences in potential harvests. The model predicts higher catch rates in the September–December fishery, originating from the April and July settlement cohorts, than in the January–June fishery, originating from the October and January settlement cohorts. The observed density of juveniles in western Florida Bay during the same years simulated by the model was greater in the fall than the spring, supporting modeling results. The observed catch rate in the fishery, a rough index of abundance, was higher in the January–June fishery than the July–December fishery in most of the biological years from 1989–1990 through 1997–1998, contrary to modeling results and observed juvenile density in western Florida Bay.

Introduction

The pink shrimp, *Farfantepenaeus duorarum*, is a good indicator of the health and productivity of the Florida Bay ecosystem. Pink shrimp in South Florida spawn offshore near the Dry Tortugas about 150 km southwest of Florida Bay, where the pink shrimp supports the multi-million dollar Tortugas shrimp fishery (Upton et al. 1992). Pink shrimp immigrate to Florida Bay as postlarvae and spend several months as juveniles feeding and growing before leaving the bay and recruiting to the commercial fishery (Costello and Allen 1966). While in Florida Bay the pink shrimp is important as a major link between the base of the food web and top consumers (Palmer 1962; Rutherford et al. 1982, 1983; Schmidt 1986, 1989; Hettler 1989).

Major changes have occurred in Florida Bay and in the harvest and recruitment characteristics of the Tortugas fishery across decades (Sheridan 1996; Ehrhardt and Legault 1999; Fourqurean and Robblee 1999). In 1987 a seagrass die-off began in western Florida Bay that was characterized by the

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rapid death of turtlegrass, *Thalassia testudinum* (Zieman et al. 1988; Robblee and DiDomenico 1991; Robblee et al. 1991a). Seagrass die-off was followed by extensive and persistent algal and turbidity blooms over much of the bay (Fourqurean et al. 1993). Loss of the estuarine nature of the bay over time and chronic hypersalinity (Zieman et al. 1988) are among the many factors hypothesized to have led to seagrass die-off. Shrimp harvests declined to period-of-record lows during the latter 1980s (Nance 1994), roughly coincident with seagrass die-off and other environmental changes in Florida Bay. This decline may in part be due to changes in freshwater inflow affecting salinity in the bay. Browder (1985) and Sheridan (1996) found statistical relationships between pink shrimp harvests and various indices of freshwater flow to the bay. Other factors affect pink shrimp in Florida Bay. Juvenile densities are strongly linked to seagrass habitats (Costello et al. 1986). Loss of seagrass habitat in the die-off resulted in local declines in seagrass-associated fishes and invertebrates including the pink shrimp (Robblee et al. 1991b; Sheridan 1992; Matheson et al. 1999).

Florida Bay lies at the downstream end of south Florida's extensive water management system. Water management to control floods, drain wetlands, and sequester water for urban and agricultural uses has altered the volume, timing, and distribution of freshwater inflow to the bay (Fennema et al. 1994; Obeysekera et al. 1999). The objective of this paper is to evaluate the relationships among freshwater inflow to Florida Bay, juvenile pink shrimp production within the bay, and shrimp harvests in the Tortugas fishery. Connecting freshwater inflow, salinity, and ecological conditions is a special challenge because of the bay's geographic complexity (Fourqurean and Robblee 1999). This paper extends the modeling work described in Browder et al. (1999). The modeling objective is to evaluate production of pink shrimp in representative regions of the bay by simulating survival and growth as functions of local water temperature and salinity. Spatial extensions of model results were made to estimate relative total potential harvests from major regions of the bay. Adjustments were then made to provide a first approximation of how bottom habitat and tidal transport might interact with salinity to affect juvenile shrimp abundance in the bay and potential harvests in the fishery.

Materials and Methods

Florida Bay

Florida Bay is a complex shallow water ecosystem at the southern tip of Florida with distinct physical and biological zones that influence the distribution and abundance of pink shrimp and other species (Fourqurean and Robblee 1999). Physically the bay is composed of many shallow basins partially separated by banks variously exposed at low tide (Holmquist et al. 1989). Banks are most extensive in the west but are more effective barriers to water exchange in the east (Enos and Perkins 1979). The principal benthic habitats in Florida Bay are seagrass beds, generally dominated by turtle grass and hard-bottom areas supporting sponges, gorgonians, corals, and macroalgae (Zieman et al. 1989; Hall et al. 1999). Seagrass development is greatest in western Florida Bay and decreases to the east following a general gradient in sediment depth. Mixed species beds are common and include both manatee grass, *Syringodium filiformi*, and shoal grass, *Halodule wrightii*. Seagrass development is locally greatest over the banks (Zieman et al. 1989). Pink shrimp occur throughout the bay (Costello and Allen 1966). Shrimp density is seasonally very high in western Florida Bay and always low in the east, closely following the patterns of seagrass. Locally pink shrimp are most abundant on bank-tops while very high densities of early settlement pink shrimp are often observed in *Halodule* grass beds (Costello et al. 1986; Robblee et al. 1991b).

Salinity patterns in the bay are influenced by the wet-dry cycle in south Florida, freshwater inflow and upstream water management, evaporation, mixing with waters of the Gulf of Mexico and the Atlantic Ocean, and internally by restricted circulation (Robblee et al. 2001). Freshwater enters eastern Florida Bay from Taylor Slough through Taylor River and other small coastal creeks (Hittle et al. 2001). Freshwater from Shark Slough and Big Cypress enter western Florida Bay after mixing with coastal waters along the southwest Florida coast (Lee et al. 2001). Because the bay is shallow, evaporation has a major influence on the bay's salt budget (Smith 2000a). Hypersaline conditions often occur by the end of the dry season (April and May). Highest salinities occur in the northern interior, where freshwater inflow is restricted by a natural coastal berm (Hittle et al. 2001) and extensive banks. Salinities exceeding 50‰ are not uncommon and can extend over much of the bay during multiyear regional droughts.

Tides, circulation, and transport in and near the bay affect not only salinity patterns but also the accessibility of various parts of the bay to pink shrimp postlarvae. Tides in Florida Bay are predominantly mixed semi-diurnal and are propagated from west to east across the bay; net water flow across the western boundary of the bay is west to east from the Gulf of Mexico to the Atlantic Ocean (Smith 2000b). Postlarval pink shrimp may maximize directional tidal transport by rising in the wa-

ter column on the flood tide and falling to the bottom on the ebb tide (Hughes 1967, 1969). Strong flood tidal currents across mud-banks and through inter-island and inter-bank channels facilitate transport into the bay (Wang et al. 1994; Wang 1998). Tidal amplitude decreases from about 60 cm in the west to a few centimeters in the east (Holmquist et al. 1989; Smith 1997). Local winds have a great influence on water level in the bay and may also influence postlarval transport (Wang et al. 1994; Wang 1998). The banks and island chains that attenuate the tide also retard mixing and transport by winds. Larval transport into interior and eastern parts of the bay may be restricted, although pink shrimp postlarvae do reach the bay's interior (Criales unpublished data).

Two routes have been proposed for transport of pink shrimp postlarvae from Tortugas spawning grounds to Florida Bay. One is that postlarvae may drift downstream with the Florida Current, entering the bay across the Lower and Middle Florida Keys. The other is that they may move northeast across the southwest Florida shelf, entering the bay at its western boundary with the Gulf of Mexico south of Cape Sable (Munro et al. 1968; Jones et al. 1970; Criales and McGowan 1994; Criales and Lee 1995). Subtidal currents are the primary mechanism linking adjacent and remote ecosystems on the inner shelf (Wang 1998) and may provide postlarval transport into Florida Bay. They are driven by local winds and offshore currents (i.e., Loop Current-Florida Current-Gulf Stream) and are strongly influenced by bathymetry and coastline orientation (Lee et al. 1994, 2001; Weisberg et al. 1996).

MODELING APPROACH

The full concept of the model under development is shown in Fig. 1. The core of the model is a unit model that simulates growth and survival of a cohort of shrimp in relation to salinity and temperature. Growth and survival are both fundamental biological processes that affect abundance and recruitment. The influence of upstream water management is expected to express itself through changes in salinity associated with change in freshwater inflow, and sensitivity to salinity variation has been demonstrated in macroinvertebrates (Kinne 1971), including other penaeids (Williams 1955, 1984; Zein-Eldin and Renaud 1986; Dall et al. 1990). Temperature was included because it is the main environmental factor affecting growth and survival, and salinity and temperature interactions have been reported in penaeids (Bielsa et al. 1983; Dall et al. 1990) and other crustaceans (Hartnoll 1982). In model simulations, shrimp that survive and attain sufficient size are considered potential
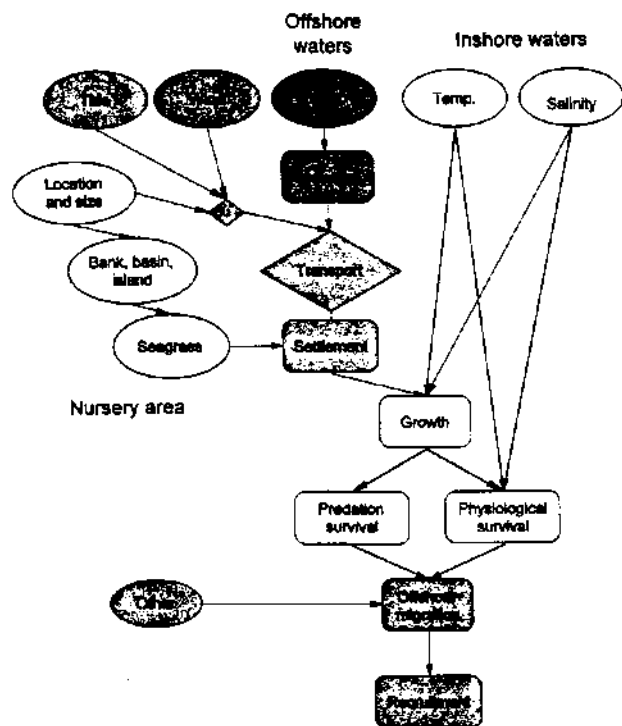

Fig. 1. Conceptual diagram of simulation model of potential recruitment from Florida Bay. Shading indicates extent of our research to date on the various model components from white (most work) to dark gray (least work).

recruits to the Tortugas fishery. The outcome of the simulations is potential harvests (mt km^{-2}) from Florida Bay. Results for each region of the bay are determined from the unit model and then expanded to the landscape scale by multiplying by the region's total area. Other conditions in Florida Bay must also be favorable to pink shrimp in order for salinity to affect growth and survival (Browder and Moore 1981; Browder 1991). For perspective on these effects, expanded results were adjusted for regional differences in physical habitat (bank, basin, or near-key), seagrass density, and an index of accessibility to postlarvae immigrating into the bay. Adjustment factors were obtained from a multiple regression analysis of existing juvenile density data.

PINK SHRIMP MODEL

The mathematical structure and scientific basis of the pink shrimp simulation model are described in detail in Browder et al. (1999). The model, written in BASIC, simulates daily growth and survival as a function of temperature and salinity. When individuals reach the age at first capture in the fishery, they are harvested at a constant fishing rate as they continue to grow and experience natural mortality, but at rates no longer affected by bay tem-

perature and salinity. Model results are dominated by three functions: growth in relation to salinity and temperature, survival in relation to salinity and temperature, and survival in relation to total length, which is a function of growth rate. These basic equations are the same as in Browder et al. (1999), however the rate coefficients, which are variables in the model, have been modified and updated as follows:

In the equation governing exponential growth as a function of salinity and temperature

$$D1 = L_{t-1}(e^{B(t)} - 1)e^{B(t-1)}, \quad \text{and } L_t = L_{t-1} + D1, \quad (1)$$

where D1 is change in total length (mm), L_t is length at day t, and L_{t-1} is length the previous day, B, the growth rate coefficient, previously B = Constant + T + T², is now

$$B \sim \text{Constant} + T + T^2 + S + S^2 + \ln L_{t-1}, \quad (2)$$

where T is water temperature, S is salinity, and L_{t-1} is total length the previous time step (day). The von Bertalanffy equation for growth (D2 in the previous model) was eliminated in this model because it was unnecessary once the variable L_{t-1} was added to the equation for B, providing a relationship between growth and size that approaches an asymptote.

In the exponential equation for the instantaneous mortality rate,

$$M1 = -\ln e^{LP} (e^{LP} + 1)^{-1}/28, \quad (3)$$

where LP, the logit transform of the survival rate, previously LP ~ Constant + T + S + T² + S² (and division was by 10), is now

$$LP \sim \text{Constant} + T + S + T^2 + S^2 + T S. \quad (4)$$

The equation for M1 back-transforms the logit to obtain the instantaneous 28-d mortality rate and then divides by 28 to obtain the instantaneous daily mortality rate. The daily survival rate from this source of mortality is calculated as

$$SV = e^{-M1}, \quad (5)$$

Regression coefficients are associated with each of the independent variables in the equations for B and LP.

The other source of mortality, predation mortality (M2), is the same in this model as in Browder et al. (1999) and is

$$M2 = A2c^{B2 L}, \quad (6)$$

where A2 = predation mortality rate at 0 mm and B2 = (ln M2$_{90}$ − ln A2)/90 (where M2$_{90}$ is predation mortality rate at 90 mm of total length).

SALINITY AND TEMPERATURE EXPERIMENTS

Two thousand juvenile pink shrimp, ranging in initial total length (TL) from 16–67 mm (mean, 36.6 mm), were collected from Florida Bay. Survival and growth were tested over a temperature range from 15°C to 33°C (15°C to 30°C at 5°C intervals) and a salinity range from 2‰ to 55‰ (5‰ intervals from 5‰ to 55‰). A treatment at 25°C and 25‰ was included in each experiment to facilitate comparisons of treatments across experiments. Ten experiments, each consisting of 4 × 5 combinations of temperature and salinity (20 treatments) were conducted. There were 200 shrimp to each experiment, with 10 assigned to each treatment, for a total of 200 trials. Animals were weighed (nearest mg) and total length was measured (nearest 0.5 mm) initially and at 7-d intervals through 28 d. Survival was determined for each trial as the percent of total individuals (adjusted by handling deaths and jump out) surviving the 28-d period. The last three experiments were conducted to compare tolerance to extreme salinity (5‰, 10‰, 45‰, 50‰, or 55‰) with and without acclimation. To acclimate, animals were introduced to the test salinity after being held at intermediate salinities for 24 to 48 h. Length of time and the number and levels of intermediate salinity were determined by the amount of difference between the ambient and test salinity.

Experimental animals were placed in individual 1000-ml beakers with aeration and fed a commercial shrimp food (Rangen 30% protein) daily, ad libidum; and feces, excess feed, exuviae, and dead animals were removed daily and recorded. Test salinities were prepared using south Florida waters, both seawater and freshwater. Salinities greater than 35‰ were prepared by adding concentrated seawater prepared from Fritz sea salts to the natural water.

Results of the 10 experiments were integrated by multiple regression analyses into equations that formed the core of the simulation model. A survival rate was obtained from the data by regression of the percent surviving at the end of each trial (logit-transformation) against temperature (second order), salinity (second order), and their interaction term. A regression equation that fitted the length-at-day (since initiation of experiment) data of each individual to an exponential equation was used to determine individual growth rate coefficients. Then a regression analysis was performed to relate individual growth rate coefficients to temperature (second order), salinity (second order), and initial total length of the individual (as the natural log). Since the data were obtained from 10 experiments, experiment was included as
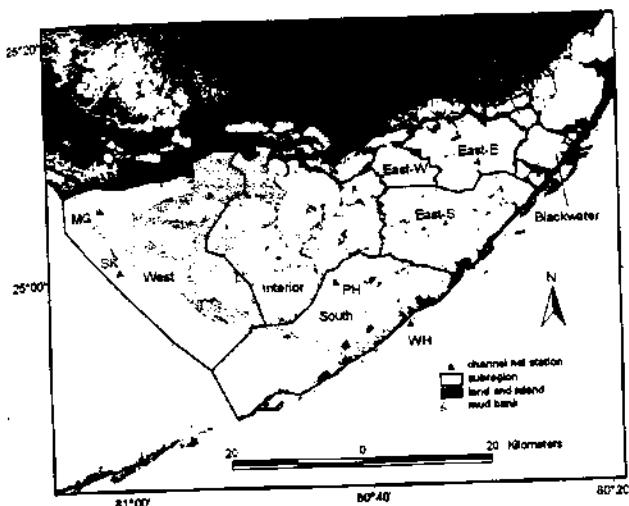
Fig. 2. Regions of Florida Bay defined for location-specific simulations of potential recruitment and harvests. Sites of present postlarval sampling to support model development. Western Bay stations are MG = Middle Ground Channel and SK = Sandy Key Channel. Southeastern Bay stations are WH = Whale Harbor Channel and PH = Panhandle Key Channel (interior station).

a categorical variable in both equations in order to remove the effect of experiment. The G-test (Sokal and Rohlf 1995) was employed to determine the effect of acclimation on survival.

SIMULATIONS

The model simulates potential harvests per unit area for regions of the bay exhibiting substantially different salinity regimes (Fig. 2) and a series of years (including years of both high and low rainfall; Fig. 3) from cohorts settling in July, October, January, and April. Recruitment to the Tortugas grounds has been described as continuous with one or more seasonal modes of variable relative magnitude and timing (Ehrhardt and Legault 1999). We attempted to represent this with our modeling. For each simulation, the model was initialized with 10 million shrimp settled km^{-2}. The number settling was distributed normally across a month of 31 d with the peak settling date at mid month, approximating the lunar periodicity in immigration and settlement (highest on the new moon) observed by previous investigators (Tabb et al. 1962; Allen et al. 1980; Criales et al. 2000). Growth and survival were simulated daily from an initial settlement size of 8.74 mm (Teinsongrusmee 1965). Young shrimp were assumed to leave the bay at 78.4 mm TL, the estimated size at which they first enter the fishery (Nichols 1984). Simulated fishing mortality began at that time, and growth and natural mortality continued through the 600th day from settlement. Harvests accumulated
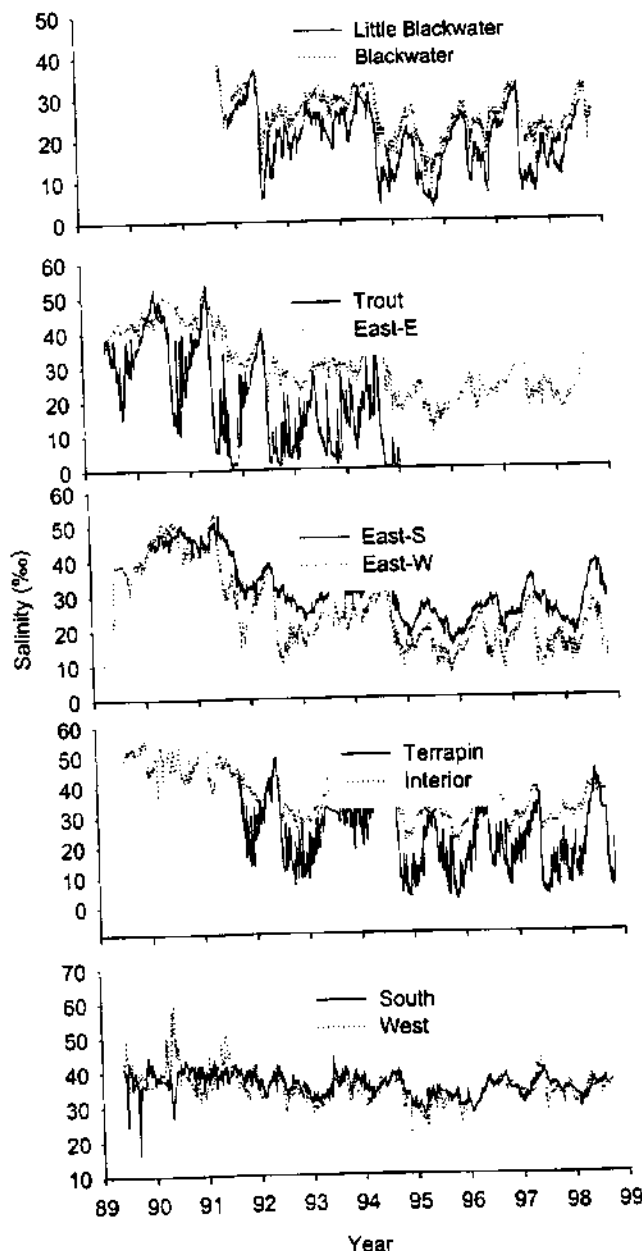

Fig. 3. Daily average salinity observed at Everglades National Park fixed monitoring stations in Florida Bay representative of salinities in bay regions of this study and some adjacent water bodies (from Smith unpublished data).

through the 600th day provided an index of potential harvest per unit area of each region. Munro et al.'s (1968) estimate of ~870 × 10^{10} protozoeal larvae produced annually on the Tortugas grounds gives perspective to the initial density we used.

Daily records from Everglades National Park fixed monitoring stations in the bay provided the temperature and salinity data used to run the model. At least one monitoring station was available for

each of the bay regions defined in this study. Data for the period June 1989 through October 1998 were used in the model.

REGIONS OF THE BAY

Representing Florida Bay as regions follows a long tradition (Turney and Perkins 1972; Wanless and Tagett 1989; Zieman et al. 1989; Boyer et al. 1997). Underlying the regions of the bay defined here is an irregular grid of basins demarcated by shallow-water mud banks with interconnecting channels that collectively represent a simplified landscape of Florida Bay (Nuttle et al. 2000). Our regions are aggregates of these basins that reflect salinity patterns in the bay and mixing with marine waters of the Gulf of Mexico and Atlantic Ocean and freshwater flows from the Florida mainland (Robblee et al. 2001). Our regions are most similar to the zones defined by Zieman et al. (1989) for seagrass and algae. The three major components of the eastern region were treated separately in our simulations because of the greater spatial and temporal variability in that region. Juvenile densities and potential harvests from four small water bodies adjacent to Florida Bay were also simulated in order to apply the model to a broader range of conditions than occurs in the bay proper. Their salinity patterns may be representative of larger estuaries of southwestern Everglades National Park known to receive immigrant pink shrimp postlarvae (Tabb et al. 1962).

ADJUSTMENTS FOR AREA AND SPATIAL VARIATION IN HABITAT AND TIDAL AMPLITUDE

The area of each of the four regions was used to expand potential harvests per unit area to the entire region. Digitized maps (spatial coverage) of physical habitat (bank, basin, and near-key), seagrass density, and zones of tidal amplitude were used to adjust for the possible effects that variation in bottom habitat and access to postlarvae might have on potential harvests from the regions of the bay. Geographic Information System (GIS) techniques were used to determine the area of each of the four regions and the proportion of each category of coverage in each region (i.e., proportion of area as bank, basin, and near-key, proportion in each seagrass density category, and proportion in each tidal amplitude zone). To make these determinations, we used coverages of banks, basins, and islands obtained from Everglades National Park, a seagrass coverage we prepared from existing data, and a map of tidal amplitude contours from Smith (1997).

The proportion of area in each seagrass density category was computed for each of our regions from a digitized seagrass map generated from several sources and representative of bottom cover in the mid to late 1990s. Point data from 1999–2000 seagrass studies in nine basins (Durako and Hall unpublished data) were used to develop a relationship between shoot density and a modified Braun-Blanquet (BB) visual index of cover, or relative density (Durako et al. 2001). Average values were computed for each station and a regression equation was constructed. BB was the dependent variable and bay region (as a categorical variable), average number of *Thalassia* shoots, average number of *Halodule* shoots, and average number of *Syringodium* shoots were the independent variables ($r^2 = 0.6182$). The resulting equation was

$$BB = 1.6877 + 0.0011TH + 0.0005HA + 0.0003SY + A, \qquad (7)$$

where BB was the Braun-Blanquet density index, TH, HA, and SY were number of short shoots of each of the three species dm^{-2}, and A was -0.4271, -0.2710, and 1.1253 for the east, interior, and west regions, respectively. We used this equation to convert average seagrass shoot density collected in 1994–1998 fishery studies by Thayer et al. (1999) and Matheson et al. (1999) to BB. Then we created the seagrass coverage from the combined data of the seagrass and fishery studies (1,116 points, produced from more than 5,000 data records).

We hypothesized that the relative accessibility of bay regions to postlarvae was related to tidal amplitude and we prepared a GIS layer of the contours of the M_2 tidal amplitude from Smith (1997) as an index of relative tidal transport. M_2 represents the lunar semi-diurnal harmonic constituent of the tide, which is the dominant tidal constituent in Florida Bay. M_2 and the other tidal constituents are greatest in the western bay and decrease from west to east.

We obtained weights for adjusting the model output for effects of regional variation in physical (bank, basin, near-key) and seagrass habitat and our index of tidal transport by analyzing an existing bay-wide juvenile pink shrimp data set of Robblee (unpublished data). He sampled juvenile pink shrimp density, JD (shrimp m^{-2}), at 54 stations in six basins from the eastern to western bay. The Robblee data set contained data on geographic location, physical habitat, and seagrass short shoot density. Seagrass density (BB) was computed using Eq. 7. We classified the data into tidal amplitude zones based on station location information. Only three zones, 1, 5, and 15, were represented in the data. Using S-PLUS, we performed multiple regression with juvenile shrimp density (ln (JD + 1)) as the dependent variable and the categorical variables, physical habitat (3 categories), seagrass density (5 categories), and tidal amplitude zone (5 cat-

egories), as independent variables. A high correlation of seagrass density with tidal amplitude and physical habitat among sites in this data set prevented us from using seagrass density in the same equation with the other two categorical variables; we made a separate equation for seagrass density. In the multiple regression analyses, computations for categorical variables were performed using the Helmert contrast matrix, which is orthogonal and produces independent contrasts unbiased by uneven sampling design (Mathsoft 1999). Once the levels were obtained for each category, we added each level to the equation's intercept and then back-transformed to obtain a predicted JD for each category. For each categorical variable, we selected the highest predicted JD and scaled the other predicted JDs to it. These computations were as follows:

$$JD = e^{l+L} - 1, \qquad (8)$$

where JD, the predicted juvenile density, is the unscaled weight for each category, l is the intercept, and L is the level for each category. The scaled weight of each category was simply JD_i/JD_{max}, where JD_{max} is the highest predicted JD for each categorical variable. The scaled weights were 1 or less.

To adjust potential harvests from our simulations for the effect of each of variable (i.e., physical habitat, BB, and tide) separately, we multiplied the scaled weight of each category (e.g., BB = 1, 2, 3, 4, or 5) by the proportion of each region covered by that category and summed the resulting products to obtain a weighting factor for that region, as follows:

$$WF_a = \Sigma(P_{ha}SW_h), \qquad (9)$$

where WF_a is the weighting factor for each region a, P_{ha} is the proportion of region a as habitat h, and SW_h is the scaled weight for habitat h. The weighting factor for a region would equal one if the most favorable category (with a scaled weight of one) covered 100% of that region. We then adjusted our simulation results for each region and year by multiplying by the region's weighting factor for that variable. We had no data for tidal amplitude zones T25 and T35, so we assigned them the same weight computed for zone T15. We did not attempt to adjust for all three variables simultaneously because the effect of seagrass density was correlated with the effects of the other two variables. It is possible that salinity regime was responsible for some of the variation attributed to physical habitat, seagrass density, and tidal-amplitude-related transport.

POSTLARVAL IMMIGRATION

In January 2000 we began monthly sampling at three sites to quantify concentrations of near-settlement-stage pink shrimp postlarvae in the water column in channels connecting Florida Bay to the Gulf of Mexico and the Atlantic Ocean (Fig. 2). A fourth site was added in June 2000. Sandy Key (SK) and Middle Ground (MG) channels are two major passes connecting the Southwest Florida Shelf to pink shrimp nursery grounds in western Florida Bay. Whale Harbor Channel (WH) connects the bay to the Atlantic Ocean, has a relatively high speed current (Smith 1998), and is the site of previous studies of pink shrimp postlarvae (Allen et al. 1980; Criales et al. 2000). Panhandle Key Channel (PH) connects the bay's interior to the outer bay and has velocities comparable to those at Whale Harbor. Based on previous studies, we sampled at night during the new moon period (Tabb et al. 1962; Allen et al. 1980; Criales et al. 2000). Two moored subsurface plankton channel nets (0.75 m² opening, 1-mm mesh net, 500-μm mesh in the cod end) were set simultaneously at each site on two consecutive nights. Nets were attached to fixed moorings and suspended with floats ~0.5 m from the surface. Cod ends were placed on the nets before dusk, and samples were collected from the cod ends shortly after dawn. A General Oceanic flow meter was mounted at the net mouth to measure velocity and flow volume through the net. Pink shrimp postlarvae were sorted from the sample, identified, and preserved in 95% ethanol. The raw catch in each sample was standardized to density per 1,000 m³ of water filtered in hours of darkness during flood tide based on Tabb et al. (1962). Mean monthly density was calculated as the average over the two sampling nights. Densities were tested for normality and homogeneity of variance.

Results

SURVIVAL IN RELATION TO SALINITY AND TEMPERATURE

Response surfaces from the 10 salinity and temperature experiments are shown in Fig. 4a,b. The regression equation for survival rate explained 46% of the variation in the predicted variable and was highly significant (Table 1). Although temperature and salinity were not significant (p > 0.05), both squared terms were highly significant, as was the interaction term (Table 1). The experiments indicated that pink shrimp have a wide salinity tolerance range but are sensitive to temperature extremes (Fig. 4a). They are especially sensitive to high salinities at low temperatures and low salinities at high temperatures. Acclimation at intermediate salinity before exposure to extreme salinity
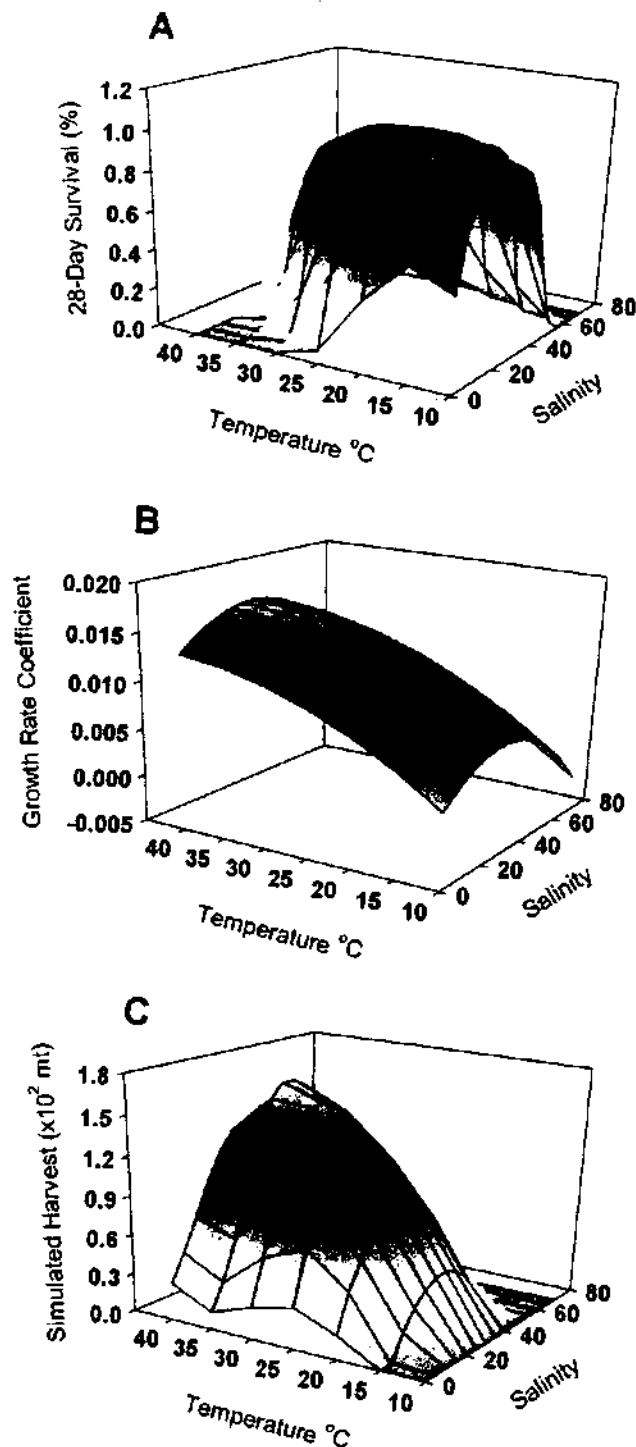
A

B

C

Fig. 4. Juvenile pink shrimp response surfaces to temperature (°C) and salinity (‰): experimentally-derived 28-d survival (proportion) (A) and daily growth rate coefficient (B) and model-simulated potential pink shrimp harvests through 600th d at constant values of temperature and salinity (C).

(5‰, 10‰, 45‰, 50‰, 55‰) had a significant (p < 0.05) beneficial effect only at 55‰. The difference was not significant at 50‰, and at 45‰ the unacclimated shrimp had higher survival rates than the acclimated shrimp. We substituted data from acclimated treatments at salinity extremes in the regression analyses in place of corresponding data from unacclimated treatments.

GROWTH IN RELATION TO SALINITY AND TEMPERATURE

The regression equation explained 71% of the variation in the individual exponential growth rate coefficients of 1,220 individuals (Table 1). This regression equation suggests that growth rate is positively related to temperature beyond 35‰ (although experiments only went to 33‰) and the salinity optimum for growth is 30‰ (Fig. 4b). The lowest growth rates were at salinity extremes at low temperatures.

GROWTH IN RELATION TO TOTAL LENGTH

The regression analysis indicated a highly significant relationship of the growth rate coefficient to total length (ln $[L^{t-1}]$) (Table 1). When used in Eq. 2 of our simulation model, the length-related coefficient of the regression equation, -0.01145 (Table 1), had such a strong negative effect on growth that shrimp did not reach recruitment size (defined as 78.4 mm TL, based on Nichols 1984) at favorable salinities and temperatures. We assumed that a size-related negative influence of confinement on growth, an artifact of the experiments (Teinsongrusmee 1965), was inflating the value of the coefficient. We substituted a smaller value, -0.00929, which allowed the model to simulate shrimp growth to a size approaching the 177.75 mm TL (maximum size $[L_\infty]$ for the von Bertalanffy growth equation in Phares 1981) within 600 d at 30‰ and 27°C.

SIMULATION MODELING

Model simulations holding temperature and salinity constant at 5°C increments from 0°C to 35°C and 5‰ intervals from 0‰ to 70‰ suggested that potential harvests are sensitive to salinity extremes (0–15‰), especially at temperatures of 15°C and lower (Fig. 4c). Simulations using observed daily temperature and salinity records from the regions of the bay (Fig. 5) suggested that potential harvests from July and April cohorts are higher and vary more than those from October and January cohorts. Year-to-year variation is greatest from the interior (93.6–151 mt km^{-2} from the July cohort) region; simulated potential harvests from the west and south regions showed a response to the driest (1989–1990 and 1990–1991)

TABLE 1. Intercepts, regression coefficients, and relative statistics of the equations for the survival and growth coefficients (determined by regression analysis of experimental data).

	Growth Rate Coefficient				Survival Rate Coefficient			
	Coef	SE	t	$Pr(>|t|)$	Coef	SE	t	$Pr(>|t|)$
Intercept	0.02908		15.35	0	−4.6019	7.0269	−0.6549	0.5135
Temp (T)	0.00832	0.00189	7.46	0	0.7039	0.5395	1.3047	0.1940
Sal (S)	0.00256	0.00011	10.65	0	0.2186	0.1408	1.5522	0.1227
T × T	-9.6×10^{-5}	2.4×10^{-5}	−4.38	0	−0.0250	0.0105	−2.3896	0.0181
S × S	-4.5×10^{-6}	2.2×10^{-6}	−10.28	0	−0.0077	0.0018	−4.3100	0.0000
T × S		4.0×10^{-7}			0.0115	0.0042	2.7763	0.0062
L_{t-1}[1]	−0.01145	0.00038	−29.88	0				
L_{t-1}[2]	−0.00929							
Df	1,205				166			
r^2	0.7095				0.4568			
F-stat	210.2			0	9.07			3.3×10^{-14}

[1] Use of this coefficient in the model yielded unrealistic results in simulations.

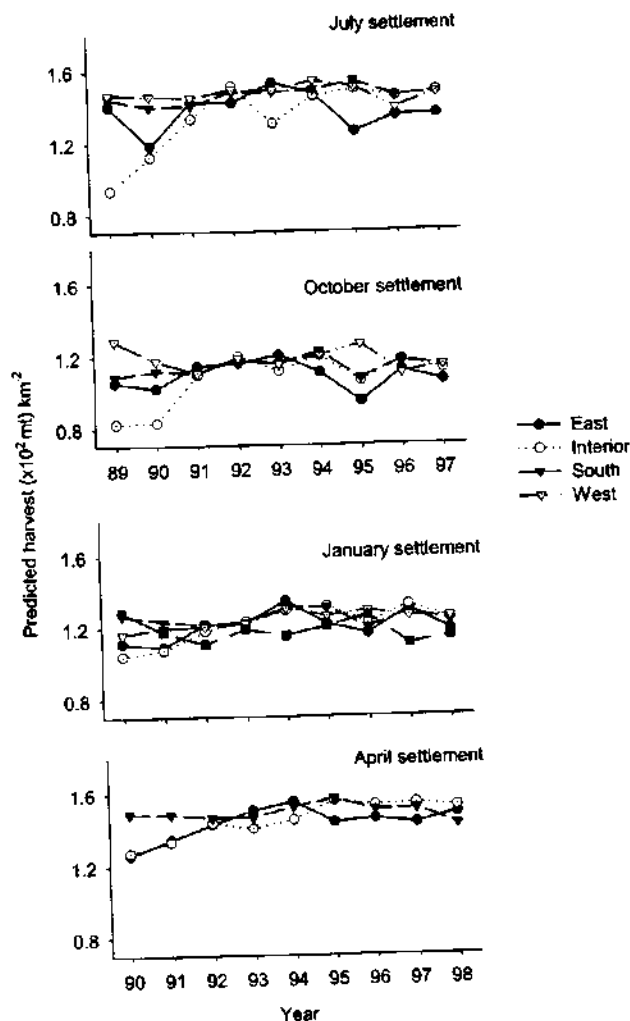[2] This value was substituted in the model.

Fig. 5. Simulated potential pink shrimp harvests per unit area of the four major Bay regions resulting from settlement cohorts in July, October, January, and April of indicated years.

and wettest (1994–1995 and 1995–1996) years. Simulated potential harvests from Trout Cove, Terrapin, and Little Blackwater and Blackwater sounds were more variable than that from the regions (61.5–153.5, 91.7–157.4, 71.6–149.7, and 126.3–156.2 mt km⁻², respectively, from the cohort settling in July).

The number of days from settlement to recruitment varied from 128 (4.25 mo) under the most favorable conditions to 175 (5.8 mo) under the least favorable conditions and also varied seasonally. The shortest periods were for the April and July cohorts, the longest, for the October and January cohorts.

Juvenile density on the grounds, viewed at 30-d intervals through 121 d, was at its maximum on day 31 when the entire cohort of that and the preceding 30 d had entered the bay. The highest 121-d density from the July-settlement cohort was 2.53 m⁻² from the western bay in 1995. The lowest 121-d density from that cohort was 1.42 m⁻² from Little Blackwater Sound, also in 1995.

EXPANSION OF UNIT-AREA RESULTS

The total nursery value of the four major regions was compared by multiplying the unit-area results for each region from the July-settlement cohort by the area of each region; results were then adjusted to account for other factors thought to influence potential recruitment and harvests (Fig. 6). The two regression equations that provided the weights used for the adjustments explained 71% (physical habitat and tidal amplitude zone) and 49% (seagrass density) of variation in the dependent variable respectively. The adjustment of potential harvests for bank, basin, and near-key area in each region had little effect, but adjustments for seagrass density coverage and tidal-amplitude zone accentuated the relative importance of the western
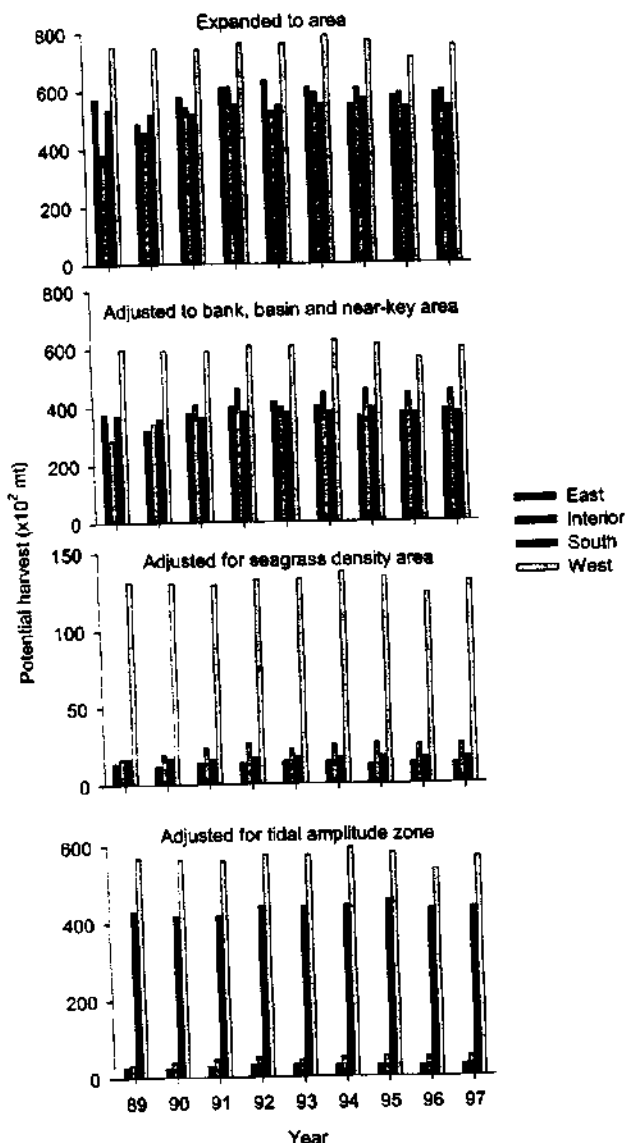
Fig. 6.   Simulated potential pink shrimp harvests of July-settlement cohort from each Bay region expanded on the basis of region area (unit area harvests × area) and adjusted for other factors thought to influence relative potential harvests from the regions of the Bay: physical habitat, seagrass density, and tidal amplitude.

TABLE 2.   Area of each region and proportion (P) covered by each indicated physical habitat type, scaled weight (SW) assigned to each habitat, and calculated weighting factor used to adjust area-expanded potential harvests for effect of spatial variation in physical habitat.

Region	Total Area (km²)	Island	Basin	Near-key	Bank	Weighting Factor
East-E	132.53	0.0729	0.9192		0.0049	0.6552
East-S	222.71	0.0721	0.8838	0.0030	0.0406	0.6654
East-W	58.17	0.0942	0.8802	0.0035	0.0223	0.6449
Interior	404.57	0.0375	0.6734	0.0033	0.2870	0.7549
South	369.86	0.0510	0.8513	0.0022	0.0947	0.6946
West	510.99	0.0137	0.6067	0.0031	0.3790	0.7956
SW		0	0.7043	1.000	0.0006	0.9720

both years, whereas Whale Harbor and Panhandle Key channels had several peaks in each year without any consistent pattern between years. The peak concentrations at Whale Harbor and Panhandle Key did not seem to be correlated. Our postlarval sampling results suggest a source of near-settlement-stage postlarvae to Florida Bay from the west in mid to late summer, roughly corresponding to the July recruitment we have simulated, and from the east and southeast at other times of the year simulated (i.e., October, January, and April). Postlarval concentrations in Whale Harbor and Panhandle channels are, however, an order of magnitude smaller than through the Middle Ground and Sandy Key channels.

Discussion

The relationships of growth and survival to temperature and salinity determined from the experiments are central to the model. Our analysis of experimental data suggested that juvenile pink shrimp survival is high over a wide salinity range except at extreme temperatures and they are least tolerant of high salinity at low temperatures and low salinity at high temperatures (Fig. 4). McKenzie (1970) reported the same relationship to temperature and salinity extremes in blue crabs. Williams (1960) noted that pink shrimp have osmoregulatory capabilities at low temperatures superior to brown shrimp. Survival at the same salinity and temperature was higher in these experiments than in our original two experiments (Browder et al. 1999). The relationship of growth to salinity in the experimental data was stronger than the relationship of survival to salinity (i.e., the r^2 was 0.71 versus 0.49). A salinity optimum (30‰) was detected within the range of salinities covered by the experiments. The temperature optimum for growth suggested by the analysis was greater than the upper temperature tested, 33°C.

Total length (the natural log) was a strong explaining variable in our equation for the growth

bay as a nursery ground. Regional areas, proportions in each habitat type, and weighting factors used in expanding and adjusting model results are shown in Tables 2, 3, and 4.

POSTLARVAL IMMIGRATION

Results of the first 20 mo of channel net sampling of immigrating postlarvae are shown in Fig. 7. Postlarval concentrations in the four channels (Fig. 2) differed in magnitude and seasonal pattern. Sandy Key and Middle Ground channels had one annual peak, centered in about July–August in

TABLE 3. Area of each region, estimated proportion of region covered by each seagrass type, proportion of region sampled, scaled weight assigned to each habitat, and calculated weighting factor used to adjust area-expanded potential harvests for effect of spatial variation in seagrass density (Braun Blanquet index, BB).

Region	Total Area (km²)	Sparse BB1	Med. Sparse BB2	Med. BB3	Med. Dense BB4	Dense BB5	Proportion of Area Sampled	Weighting Factor
East-E	132.54	0.9381	0.0619	0	0	0	0.0026	0.0128
East-S	222.71	0.6190	0.3756	0.0055	0	0	0.4469	0.0190
East-W	58.17	0.8387	0.0072	0.1541	0	0	0.8926	0.0675
Interior	404.57	0.2545	0.6878	0.0561	0.0016	0	0.7367	0.0430
South	369.86	0.0739	0.9064	0.0176	0	0	0.3929	0.0313
West	510.99	0.0129	0.7586	0.1167	0.1044	0.0075	0.4101	0.1743
Total	1,698.82						0.1234	
Scaled weight (SW)		0.0120	0.0254	0.3715	1.0000	0.9856		

rate coefficient. Part of this effect was apparently an artifact of the experiment because it was not possible, using the model, to simulate growth from early settlement to recruitment size shrimp at ambient salinities and temperatures using the coefficients generated from the regression analysis (Eq. 2, Table 1). We had our choice of modifying either the intercept of the regression equation or the regression coefficient controlling the effect of total length. By changing only the regression coefficient for L_{t-1}, we approached the L_z of Phares (1981) within the 600-d simulation period. Growth from settlement to recruitment size (137 d at 27°C and 30‰) with this model was slower than with previous versions of the model, in which recruitment size was reached in about 100 d.

Other estimates of time from settlement to recruitment vary for this species in South Florida. Tabb et al. (1962) reported estimated growth rates consistent with the slower growth of our model. Kutkuhn (1966) estimated 3–4 wk (21–28 d) from spawning to settlement and 10–11 wk (70–77 d) from settlement to recruitment. Costello and Allen (1970) said that 2–6 mo is spent in the shallow nursery areas. Estimates of size at recruitment also vary from 78.4 mm TL (Nichols 1984), which we used, to about 100 mm TL (Joyce 1965; Kutkuhn 1966). Pink shrimp larger than 17 mm carapace length (CL; ~84 mm TL) are seldom seen in John-

son Key Basin, a western Florida Bay nursery ground (only 1.4% of shrimp captured in routine collections exceeded 17 mm CL; Robblee unpublished data).

Acclimation's lack of a significant influence at any but the highest salinity tested was surprising. There are several possible reasons. The difference in survival between acclimated and unacclimated shrimp in each trial might have been too small to be resolved by the sample size of our experiments. Individual variation in tolerance may have been too great to allow relatively small differences between treatments to be distinguished. Alternatively, salinity of at least 55‰ (the highest salinity tested) may have been required to trigger acclimation. There's a practical reason why pink shrimp in Florida Bay might have the ability to acclimate to high salinity but lack the ability to acclimate to low salinity. Hypersaline conditions develop gradually, allowing time for acclimation, whereas salinity sometimes decreases rapidly in response to heavy rains and freshwater inflow, leaving no time to acclimate.

The salinity optimum of 30‰ has ecological significance in Florida Bay. Salinities of approximately 30‰ occur in some years, even in the western bay. Salinities both below and, more often, above 30‰ often prevail in the interior bay. Salinities above and, more often, below 30‰ occur in the eastern

TABLE 4. Area of reach region, proportion in each indicated tidal amplitude zone, scaled weight for each zone, and calculated weighting factor used to adjust area-expanded potential harvests for effect of spatial variation in tidal-amplitude-related transport of postlarvae.

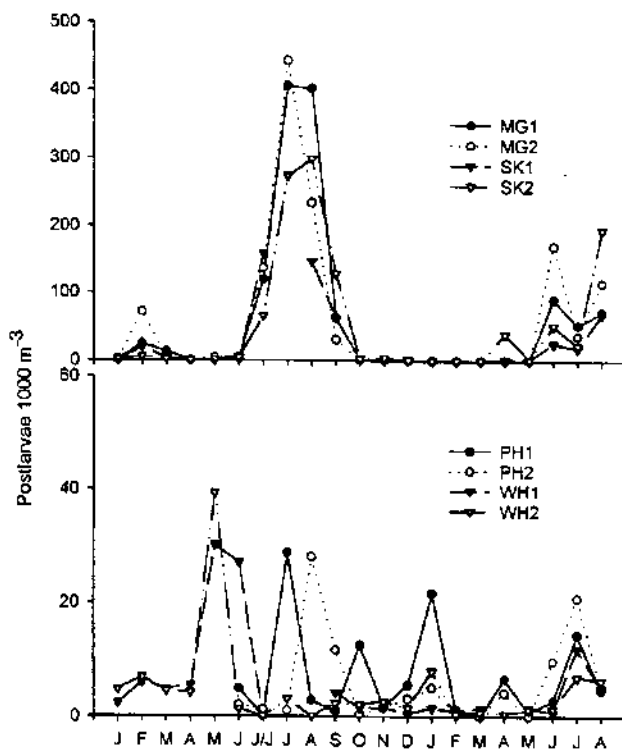| Region	Total Area (km²)	1-cm	5-cm	15-cm	25-cm	35-cm	Weighting Factor
East-E	132.54	1.0000	0	0	0	0	0
East-S	222.71	0.3473	0.5848	0.0670	0	0	0.0925
East-W	58.17	1.0000	0	0	0	0	0
Interior	404.57	0.1634	0.7843	0.0511	0.0006	0	0.0859
South	369.86	0.0000	0.1857	0.7455	0.0522	0	0.8058
West	510.99	0.0000	0.0599	0.2356	0.2417	0.2757	0.7556
Total	1698.82						
Scaled weight (SW)		0.0000	0.0436	1	1	1	

Fig. 7. Observed concentrations of pink shrimp postlarvae in western (MG, SK) and eastern (PH, WH) Florida Bay Channels (see Fig. 2 for locations) during new-moon sampling, January 2000 through August 2001.
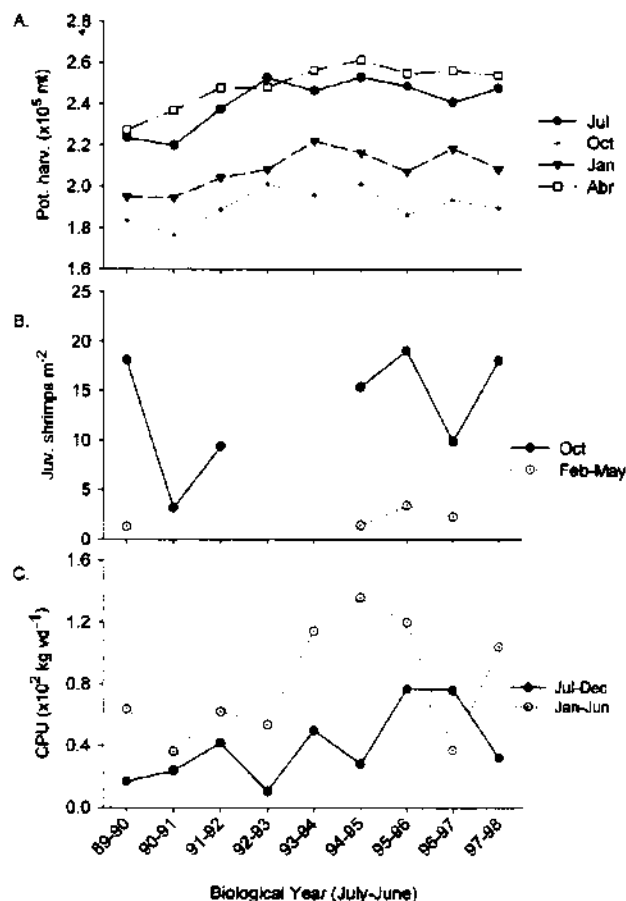

Fig. 8. Simulated potential harvests from each cohort from all four regions, expanded by area (A), observed juvenile pink shrimp density on western Florida Bay nursery grounds (Robblee unpublished data) in October and within the period February–May (B), and observed CPUE (10^2 kg vd^{-1}, where vd is vessel day) of pink shrimp recruits (smallest commercial size class category) in the Tortugas fishery for 6-mo period, January–June and July–December, by biological (July–June) year (C).

bay. Periods of near 30‰ salinity are reflected in higher juvenile densities, shorter times from settlement to recruitment, and larger potential harvests. The differences are smaller than we expected based on Browder et al. (1999).

The shape of the response surface of potential harvest in relation to salinity and temperature (Fig. 4c) suggests potential harvests are more sensitive to salinity and temperature than would be expected based on the response surfaces of either survival or growth alone (Fig. 4a,b). This is because modeling results are the integrated effect of three processes, physiologically based physiological survivorship, growth, and a size-dependent survival from predation.

We selected July, October, January, and April as settlement months to examine the effect of seasonal variation in temperature and salinity on potential harvests from the bay. The July settlement date also corresponds well with the July–August-centered peaks in settlement-stage postlarval concentrations in the western bay observed in our field sampling (Fig. 7). We found peak concentrations of near-settlement-stage postlarvae in Whale Harbor and Panhandle Key Channels at other times of the year, suggesting that settlement stage postlarvae may be available in the other months we sim-

ulated (October, January, and April). These peaks were much lower than in the western bay in July–August. Tabb et al. (1962) also noted peaks of abundance of settlement-stage postlarvae at several times of the year.

Relative harvests expanded to the four-region area (1,699 km^2) are shown for each cohort and each year in Fig. 8a for comparison with observed juvenile densities at corresponding times of the year (Fig. 8b). At the growth rates of our simulations, the July-settlement cohort was on the nursery grounds in October, a time when peak densities of juvenile pink shrimp are commonly observed in sampling (Robblee unpublished data; Fig. 8b).

We looked at a proxy of recruitment, the monthly average catch rate (kg vd^{-1}, where vd is vessel day) of the youngest commercial size class in the
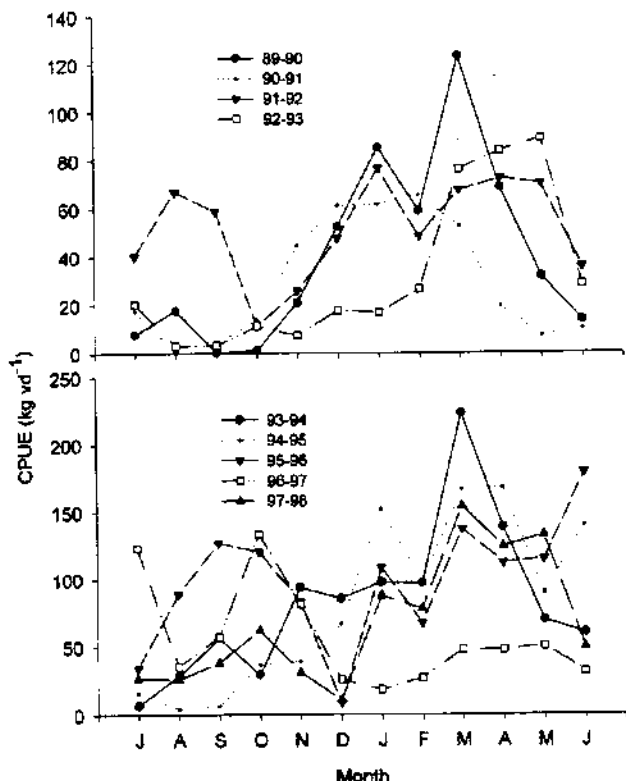
Fig. 9. Monthly observed average catch per unit of effort (CPUE; kg vd^{-1}, where vd is vessel day) of recruits (commercial catch category $\geq$ 31 shrimp kg^{-1}) in Tortugas pink shrimp harvests, by biological (July–June) year, 1989–1990 through 1997–1998.

fishery (68-count-per-pound, or 31 kg^{-1} shrimp) in relation to our simulation results. Our simulations initialized with cohorts settling in the bay in July, October, January, and April produced modes of recruitment roughly corresponding in timing to those observed in fishery harvests. Two or more recruitment modes were observed in most years from 1989–1990 through 1997–1998 (Fig. 9). Our July-settlement cohort produced an early-December peak in simulated recruitment to the fishery. Our October-settlement cohort produced recruits corresponding to the March–April maximum in observed catch rates of recruits in the fishery. The January-settlement cohort simulated by the model recruited to the fishery in June. This corresponds to the June peak in recruitment in landings data in some years (Fig. 9). Our April cohort recruited to the fishery in August. A May cohort might better approximate the September recruitment sometimes seen in the fishery.

By separating the data into 6-mo periods and plotting it by year (Fig. 8c), we find that catch rates are highest in the January–June period in every year but one. Our simulations differed from fishery data by consistently producing higher potential

harvests from the April and July settlement cohorts (Fig. 8a), which recruited to the fishery from August through December. The year-to-year variation in our simulated potential harvests, expanded to the area of the bay, is too small (with or without adjustment for regional variation in seagrass density) to account for the year-to-year variation in magnitude of the various modes of recruitment to the fishery.

Despite the presence of several modes in the fishery, there is no direct evidence that pink shrimp in the Tortugas exhibit the bimodal spawning described for some tropical penaeid shrimps (Dall et al. 1990; Crocos 1991). Pink shrimp females in spawning condition are found year around; the frequency of ripe females is highest from April through July (Cummings 1961). Early larval stages at the Dry Tortugas also have been found year around and concentrations were highest from April to July (Munro et al. 1968; Jones et al. 1970).

The model simulations were initialized for all four cohorts with the same number of settlement-stage postlarvae. In reality, postlarvae arrive at the bay in waves related to the new moon. These waves are of greater magnitude in some months than others due to variation in spawning strength and oceanographic conditions that affect onshore transport. This might explain differences in the relative importance of cohorts in the model and the fishery. Some other explanations are needed for the differences in relative importance of cohorts between the observed juvenile densities in the bay and catch rates in the fishery. Differences in timing of subadults leaving the bay relative to their size might account for these differences. At present the model does not allow shrimp size to vary at emigration, which Tabb et al. (1962) have documented in relation to storms and sudden decreases in salinity or temperature. Environmental control of natural mortality and growth rates outside the bay could also account for some of the variation in fishery catch rates. The model at present does not address the possible influence of monthly and annual variation in temperature and salinity outside of Florida Bay. Constant values of temperature (27°C) and salinity (35‰) are used to govern survival and growth beyond 78.4 mm, when they leave the bay in the model. This is because our focus has been on the effect of conditions in the bay, but extending the effect of salinity and temperature to cover the rest of the growth and life cycle of the cohorts and using observed salinity and temperature data from offshore waters might alter simulation results.

The unit model has immediate application in designing a monitoring program for the Compre-

hensive Everglades Restoration Project (U.S. Army Corps of Engineers 1999), which will restructure South Florida's water management system and may change the volume, timing, and distribution of freshwater flows to Florida Bay. A dynamic monitoring strategy could be guided by model predictions of where and when peak densities of juvenile pink shrimp at various stages of growth and development will appear and the relative magnitude and timing of potential recruitment. The model may also be used in a hindcasting mode to help interpret monitoring results in terms of impacts. Predictions and hindcasts would be based on current information on rainfall, freshwater inflow, and other environmental factors.

We expanded results of our unit model to the full area of the bay to better evaluate their implications. Using information from field studies to adjust our modeling results for other factors known to affect pink shrimp densities in the bay contributed further perspective. Our conclusion following adjustments is that salinity variation in the eastern bay may be irrelevant to shrimp production because of the relatively low bank area, seagrass density, and tidal-amplitude-related access to postlarvae. The salinity extremes (especially high salinity) prone to occur in interior Florida Bay diminish its value as a pink shrimp nursery ground. A reduction in the frequency, duration, and spatial extent of hypersaline conditions would improve the production potential of the interior bay. Even with optimal salinities, the interior bay probably would not be as valuable a pink shrimp nursery ground as western Florida because of lower seagrass densities and lower tidal-amplitude-related postlarval immigration opportunity. The production potential of western Florida Bay is relatively stable from year to year, but an increase in the frequency and duration of salinities of about 30‰ would be expected to increase the potential harvests from this area if it did not detrimentally affect seagrass habitat.

Both growth and survival of juvenile pink shrimp are favored by an absence of salinity extremes. Because of spatial and temporal variability in conditions and habitat and given its broad salinity tolerance range, this species should be able to survive and grow somewhere in Florida Bay or nearby estuaries whenever postlarvae arrive from offshore spawning grounds. One key to maintaining a high production of this species is maintaining freshwater inflow that will provide a favorable salinity range over the greatest amount of suitable and accessible habitat at these critical times. Conditions also must be maintained to promote moderately high to high seagrass density and cover in areas accessible to pink shrimp postlarvae. Model results suggested that the higher freshwater flows associated with higher rainfall that occurred from late 1994 through 1996 extended favorable salinities for pink shrimp over the greatest area of Florida Bay. Lower flows associated with the lower rainfall of 1989 through 1991 reduced the area of favorable salinities. Fundamental changes in water management would increase the productive capacity of the bay to the extent it could decrease the frequency, intensity, duration, and spatial coverage of hypersaline events in the bay. Extremely low salinities have an even more detrimental effect on pink shrimp than do high salinities; however, over the nine years examined, salinities low enough to be detrimental occurred in the bay only where unfavorable habitat and low accessibility would also restrict pink shrimp production. Production from the estuaries of southwestern Everglades National Park might be detrimentally affected by high flows. Timing of flows in relation to postlarval immigrations is important.

Our integration of laboratory experiments with a simulation model and comparison with field and fishery observations raises questions that will guide new investigations. Relative abundance and the timing of abundance peaks at various life stages warrant further work. More detailed field observations of the reproductive output of the Dry Tortugas pink shrimp population are necessary to determine seasonal and annual patterns of the availability of postlarvae. Longer time series are needed to better characterize the timing and magnitude of immigration into the bay and determine influencing factors. The timing and pattern of juvenile emigration from Florida Bay is an unknown and priority need. Addressing timing issues by integrating field and fishery observations is an appropriate future role for the simulation model. Results of our adjustments suggest that a landscape-based model is needed to more fully examine the dynamic overlap of salinity, bottom habitat, and accessibility to postlarvae. More bay-wide data on the distribution of juvenile density should be acquired to jointly estimate effects of spatial variation in physical habitat, seagrass density, and tidal-amplitude-related access to postlarvae.

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LITERATURE CITED

ALLEN, D. M., J. H. HUDSON, AND T. J. COSTELLO. 1980. Postlarval shrimp (*Penaeus*) in the Florida Keys, species, size, and seasonality. *Bulletin of Marine Science* 30:21–33.

BIELSA, L. M., W. H. MURDICH, AND R. F. LABISKY. 1983. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (South Florida) pink shrimp. Biological Report FWS/OBS-82/11. U.S. Fish and Wildlife Service, Washington, D.C.

BOYER, J. N., J. W. FOURQUREAN, AND R. D. JONES. 1997. Spatial characterization of water quality in Florida Bay and Whitewater Bay by multivariate analyses: Zones of similar influence. *Estuaries* 20:743–758.

BROWDER, J. A. 1985. Relationship between pink shrimp production on the Tortugas grounds and water flow patterns in the Florida Everglades. *Bulletin of Marine Science* 37:839–856.

BROWDER, J. A. 1991. Watershed management and the importance of freshwater flow to estuaries, p. 7–22. *In* S. F. Treat and P. A. Clark (eds.), BASIS II, Proceedings of the Tampa Bay Area Scientific Information Symposium 2, 27 February–1 March 1991. TEXT, Tampa, Florida.

BROWDER, J. A. AND D. MOORE. 1981. A new approach to determining the quantitative relationship between fishery production and the flow of fresh water to estuaries, p. 403–430. *In* R. Cross and D. Williams (eds.), Proceedings of the National Symposium on Freshwater Inflow to Estuaries, Volume 1. FWS/OBS-81/04. U.S. Fish and Wildlife Service, Washington, D.C.

BROWDER, J. A., V. R. RESTREPO, J. K. RICE, M. B. ROBBLEE, AND Z. ZEIN-ELDIN. 1999. Environmental influences on potential recruitment of pink shrimp, *Farfantepenaeus duorarum*, from Florida Bay nursery grounds. *Estuaries* 22:484–499.

COSTELLO, T. J. AND D. M. ALLEN. 1966. Migrations and geographic distribution of pink shrimp, *Penaeus duorarum*, of the Tortugas and Sanibel grounds, Florida. *Fishery Bulletin U.S.* 65:449–459.

COSTELLO, T. J. AND D. M. ALLEN. 1970. Synopsis of biological data on pink shrimp, *Penaeus duorarum duorarum* Burkenroad, 1939. FAO Fishery Report No. 57, p. 1499–1537, Volume 4. Food and Agricultural Organization, Rome, Italy.

COSTELLO, T. J., D. M. ALLEN, AND J. H. HUDSON. 1986. Distribution, seasonal abundance, and ecology of juvenile northern pink shrimp, *Penaeus duorarum*, in the Florida Bay area. NOAA Technical Memorandum NMFS-SEFC-161. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida.

CRIALES, M. M., M. J. BELLO, AND C. YEUNG. 2000. Diversity and recruitment of penaeoid shrimps at Bear Cut, Biscayne Bay, Florida, USA. *Bulletin of Marine Science* 67:773–788.

CRIALES, M. M. AND T. N. LEE. 1995. Larval distribution and transport of penaeid shrimps during the presence of the Tortugas Gyre in May–June 1991. *Fishery Bulletin U.S.* 93:471–482.

CRIALES, M. M. AND M. F. MCGOWAN. 1994. Horizontal and vertical distribution of penaeidean larvae and micronektonic shrimps in the Florida Keys. *Bulletin of Marine Science* 54:843–856.

CROCOS, P. 1991. Reproductive dynamics of three species of Penaeidae in tropical Australia, and the role of reproductive studies in fisheries management, p. 317–331. *In* A. Wenner and A. Kuris (eds.), Crustacean Egg Production, Crustacean Issues 7. Balkema, Rotterdam, Netherlands.

CUMMINGS, W. C. 1961. Maturation and spawning of the pink shrimp, *Penaeus duorarum* Burkenroad. *Transactions of the American Fishery Society* 90:462–468.

DALL, W., B. J. HILL, P. C. ROTHLISBERG, AND D. J. SHARPLES. 1990. The Biology of the Penaeidae. Advances in Marine Biology, Volume 27. Academic Press, London, U.K.

DURAKO, M. J., M. O. HALL, AND M. MERELLO. 2001. Patterns of change in the seagrass-dominated Florida Bay hydroscape, p. 523–538. *In* J. W. Porter and K. G. Porter (eds.), The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Boca Raton, Florida.

EHRHARDT, N. M. AND C. M. LEGAULT. 1999. Pink shrimp, *Farfantepenaeus duorarum*, recruitment variability as an indicator of Florida Bay dynamics. *Estuaries* 22:471–483.

ENOS, P. AND R. D. PERKINS. 1979. Evolution of Florida Bay from island stratigraphy. *Geological Society of America Bulletin* 90:59–83.

FENNEMA, R. J., C. J. NEIDRAUER, R. A. JOHNSON, T. K. MACVICAR, AND W. A. PERKINS. 1994. A computer model to simulate natural Everglades hydrology, p. 249–289. *In* S. M. Davis and J. C. Ogden (eds.), Everglades: The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, Florida.

FOURQUREAN, J. W., R. D. JONES, AND J. C. ZIEMAN. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. *Estuarine, Coastal and Shelf Science* 36:295–314.

FOURQUREAN, J. W. AND M. B. ROBBLEE. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22:345–357.

HALL, M. O., M. J. DURAKO, J. W. FOURQUREAN, AND J. C. ZIEMAN. 1999. Decadal changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22:445–459.

HARTNOLL, R. G. 1982. Growth, p. 111–196. *In* D. Bliss (ed.), The Biology of Crustacea. Embryology, Morphology, and Genetics, Volume 2. Academic Press, London, U.K.

HETTLER, JR., W. F. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bulletin of Marine Science* 44:155–162.

HITTLE, C. D., E. PATINO, AND M. ZUCKER. 2001. Freshwater flow from estuarine creeks into northeastern Florida Bay. Water Resources Investigation Report No. 01-4164. U.S. Geological Survey, Miami, Florida.

HOLMQUIST, J. G., G. V. N. POWELL, AND S. M. SOGARD. 1989. Sediment, water level and water temperature characteristics of Florida Bay's grass-covered mud banks. *Bulletin of Marine Science* 44:348–364.

HUGHES, D. A. 1967. On the mechanisms underlying tide associated movements of *Penaeus duorarum*. Contribution to the Food and Agricultural Organization World Scientific Conference on the Biology and Culture of Shrimps and Prawns, Mexico City, Food and Agricultural Organization, Rome. *FAO Fishery Report* 67:971–981.

HUGHES, D. A. 1969. Responses to salinity changes as a tidal transport mechanism of pink shrimp, *Penaeus duorarum*. *Biological Bulletin* 136:43–53.

JONES, A. C., D. E. DIMITRIOU, J. J. EWALD, AND J. H. TWEEDY. 1970. Distribution of early developmental stages of pink shrimp, *Penaeus duorarum*, in Florida waters. *Bulletin of Marine Science* 20:634–661.

JOYCE, JR., E. A. 1965. The commercial shrimps of the northeast coast of Florida. Professional Paper Series No. 6. Florida State Board of Conservation Marine Laboratory, St. Petersburg, Florida.

KINNE, O. 1971. Invertebrates, p. 821–995. *In* H. Barnes (ed.), Marine Ecology, Volume 1, Part 2. Wiley-Interscience, New York.

KUTKUHN, J. H. 1966. Dynamics of a penaeid shrimp population and management implications. *Fishery Bulletin U.S.* 65:313–338.

LEE, T., M. E. CLARKE, E. WILLIAMS, A. F. SZMANT, AND T. BERGER. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science* 54: 621–646.

LEE, T. N., E. JOHNS, D. WILSON, E. WILLIAMS, AND N. P. SMITH. 2001. Transport processes linking south Florida coastal ecosystems, p. 309–342. *In* J. W. Porter and K. G. Porter (eds.). The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, Florida.

MATHESON, JR., R. E., D. K. CAMP, S. M. SOGARD, AND K. A. BJORGO. 1999. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: The effects of recent ecosystem changes? *Estuaries* 22:534–551.

MATHSOFT. 1999. S-PLUS 2000 Modern Statistics and Advanced Graphics Guide to Statistics, Volume 1. Insightful, Seattle, Washington.

MCKENZIE, M. D. 1970. Fluctuations in abundance of the blue crab and factors affecting mortalities. South Carolina Marine Research Division Technical Report 1. South Carolina Department of Natural Resources, Charleston, South Carolina.

MUNRO, J. L., A. C. JONES, AND D. DIMITRIOU. 1968. Abundance and distribution of the larvae of the pink shrimp (*Penaeus duorarum*) on the Tortugas Shelf of Florida, August 1962–October 1964. *Fishery Bulletin U.S.* 67:165–181.

NANCE, J. M. 1994. A biological review of the Tortugas pink shrimp fishery through December 1993. Galveston Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, Galveston, Texas.

NICHOLS, S. 1984. Updated assessment of brown, white, and pink shrimp in the United States Gulf of Mexico. Miami Laboratory, Southeast Fisheries Science Center, National Marine Fisheries service, Miami, Florida.

NUTTLE, W. K., J. W. FOURQUREAN, B. J. COSBY, J. C. ZIEMAN, AND M. B. ROBBLEE. 2000. Influence of net freshwater supply on salinity in Florida Bay. *Water Resources Research* 36:1805–1822.

OBEYSEKERA, J., J. A. BROWDER, L. HORNUNG, AND M. A. HARWELL. 1999. The natural South Florida system I: Climate, geology, and hydrology. *Urban Ecosystems* 3:223–244.

PALMER, R. S. 1962. Handbook of North American Birds I. Yale University Press, New Haven, Connecticut.

PHARES, P. L. 1981. Aspects of the pink shrimp fishery in the eastern Gulf of Mexico for the years 1960–1979. Miami Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, Florida.

ROBBLEE, M. B., T. R. BARBER, P. R. CARLSON, JR., M. J. DURAKO, J. W. FOURQUREAN, L. K. MUEHLSTEIN, D. PORTER, L. A. YARBRO, R. T. ZIEMAN, AND J. C. ZIEMAN. 1991a. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71:297–299.

ROBBLEE, M. B., G. CLEMENT, D. SMITH, AND R. HALLEY. 2001. Salinity pattern in Florida Bay: A synthesis (1900–2000), p. 34–36. *In* Proceedings 2001 Florida Bay Science Conference, Key Largo, Florida, April 23–26. 2001. University of Florida, Gainesville, Florida.

ROBBLEE, M. B. AND W. J. DIDOMENICO. 1991. Seagrass die-off threatens ecology of Florida Bay. *Park Science* 11:21–22.

ROBBLEE, M., S. D. JEWELL, AND T. W. SCHMIDT. 1991b. Temporal and spatial variation in the pink shrimp, *Penaeus duorarum*, in Florida Bay and adjacent waters of Everglades National Park. Annual Report. South Florida Research Center, Everglades National Park, Homestead, Florida.

RUTHERFORD, E. S., E. B. THUE, AND D. G. BUKER. 1982. Population characteristics, food habitats and spawning activity of the spotted seatrout, *Cynoscion nebulosus*, in Everglades National Park, Florida. U.S. National Park Service. South Florida Research Center Report T-688. Everglades National Park, Homestead, Florida.

RUTHERFORD, E. S., E. B. THUE, AND D. G. BUKER. 1983. Population characteristics, food habitats and spawning activity of the gray snapper, *Lutjanus griseus*, in Everglades National Park, Florida. U.S. National Park Service. South Florida Research Center Report SFRC-83/02. Everglades National Park, Homestead, Florida.

SCHMIDT, T. W. 1986. Food of young juvenile lemon sharks, *Negaprion brevirostris*, near Sandy Key, western Florida Bay. *Florida Scientist* 49:7–10.

SCHMIDT, T. W. 1989. Food habits, length-weight relationship, and condition factor of young great barracuda, *Sphyraena barracuda*, (Walbaum) from Florida Bay, Everglades National Park, Florida. *Bulletin of Marine Science* 44:163–170.

SHERIDAN, P. F. 992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. *Bulletin of Marine Science* 50:21–39.

SHERIDAN, P. F. 1996. Forecasting the fishery for pink shrimp, *Penaeus duorarum*, on the Tortugas grounds, Florida. *Fishery Bulletin U.S.* 94:743–755.

SMITH, N. P. 1997. An introduction to the tides of Florida Bay. *Florida Scientist* 60:53–67.

SMITH, N. P. 1998. Tidal and long-term exchanges through channels in the middle and upper Florida Keys. *Bulletin of Marine Science* 62:199–211.

SMITH, N. P. 2000a. Evaporation and the precipitation-evaporation balance in Florida Bay. *Florida Scientist* 63:72–83.

SMITH, N. P. 2000b. Transport across the western boundary of Florida Bay. *Bulletin of Marine Science* 66:291–304.

SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry, 3rd edition. W. H. Freeman, New York.

TABB, D. C., D. L. DUBROW, AND A. E. JONES. 1962. Studies on the biology of the pink shrimp, *Penaeus duorarum* Burkenroad, in Everglades National Park, Florida. Florida Board of Conservation Technical Series No. 37. Florida State Board of Conservation, Tallahassee, Florida.

TEINSONGRUSMEE, B. 1965. The effect of temperature on growth of post-larval pink shrimp, *Penaeus duorarum* Burkenroad. Masters Thesis, University of Miami, Coral Gables, Florida.

THAYER, G. W., A. B. POWELL, AND D. E. HOSS. 1999. Composition of larval, juvenile, and small adult fishes relative to changes in environmental conditions in Florida Bay. *Estuaries* 22:518–533.

TURNEY, W. J. AND B. F. PERKINS. 1972. Molluscan Distribution in Florida Bay. Sediments III. University of Miami, Miami, Florida.

U.S. ARMY CORPS OF ENGINEERS. 1999. Central and southern Florida project comprehensive review study. Final report. U.S. Army Corps of Engineers, Jacksonville District, Jacksonville, Florida.

UPTON, H. F., P. HOAR, AND M. UPTON. 1992. The Gulf of Mexico Shrimp Fishery: Profile of a Valuable National Resource. Center for Marine Conservation, Washington, D.C.

WANG, J. D. 1998. Subtidal flow patterns in western Florida Bay. *Estuarine, Coastal and Shelf Science* 46:901–15.

WANG, J. D., J. VAN DE KREEKE, N. KRISHNAN, AND D. SMITH. 1994. Wind and tide response in Florida Bay. *Bulletin of Marine Science* 54:579–601.

WANLESS, H. R. AND M. G. TAGETT. 1989. Origin, growth and evolution of carbonate mudbanks in Florida Bay. *Bulletin of Marine Science* 44:454–489.

WEISBERG, R. H., B. D. BLACK, AND J. YANG. 1996. Seasonal modulation of the West Florida continental shelf circulation. *Journal of Geophysical Research* 23:2247–2250.

WILLIAMS, A. B. 1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. *Bulletin of Marine Science Gulf and Caribbean* 5:116–146.

WILLIAMS, A. B. 1960. The influence of temperature on osmotic regulation in two species of estuarine shrimps (*Penaeus*). *Biological Bulletin* 118:560–571.

WILLIAMS, A. B. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast. Smithsonian Institution Press, Washington, D.C.

ZEIN-ELDIN, Z. P. AND M. L. RENAUD. 1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus* populations in coastal waters, particularly of Texas. *Marine Fishery Reviews* 48:9–19.

ZIEMAN, J. C., J. W. FOURQUREAN, AND R. L. IVERSON. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292–311.

ZIEMAN, J. C., J. W. FOURQUREAN, M. B. ROBBLEE, M. DURAKO, P. CARLSON, L. YARBRO, AND G. POWELL. 1988. A catastrophic die-off of seagrasses in Florida Bay and Everglades National Park: Extent, effect and potential causes. *EOS* 69:1111.

SOURCES OF UNPUBLISHED MATERIALS

DURAKO, M. unpublished data. Center for Marine Science, University of North Carolina at Wilmington, Wilmington, North Carolina.

HALL, M. O. unpublished data. Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida.

SMITH, D. unpublished data. National Park Service, Everglades National Park, 40001 State Road 9336, Homestead, Florida 33030.